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## Evolutionary dynamics of a common sub-Antarctic octocoral family



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## ABSTRACT

Sequence data were obtained for five different loci, both mitochondrial (cox1, mtMutS, 16S) and nuclear (18S, 28S rDNA), from 64 species representing 25 genera of the common deep-sea octocoral family Primnoidae. We tested the hypothesis that Primnoidae have an Antarctic origin, as this is where they currently have high species richness, using Maximum likelihood and Bayesian inference methods of phylogenetic analysis. Using a time-calibrated molecular phylogeny we also investigated the time of species radiation in sub-Antarctic Primnoidae.

Our relatively wide taxon sampling and phylogenetic analysis supported Primnoidae as a monophyletic family. The base of the well-supported phylogeny was Pacific in origin, indicating Primnoidae sub-Antarctic diversity is a secondary species radiation. There is also evidence for a subsequent range extension of sub-Antarctic lineages into deep-water areas of the Indian and Pacific Oceans.

Conservative and speculative fossil-calibration analyses resulted in two differing estimations of sub-Antarctic species divergence times. Conservative analysis suggested a sub-Antarctic species radiation occurred ~52 MYA (95% HPD: 36–73 MYA), potentially before the opening of the Drake Passage and Antarctic Circumpolar Current (ACC) formation (41–37 MYA). Speculative analysis pushed this radiation back into the late Jurassic, 157 MYA (95% HPD: 118–204 MYA).

Genus-level groupings were broadly supported in this analysis with some notable polyphyletic exceptions: *Callogorgia*, *Fanellia*, *Primnoella*, *Plumarella*, *Thouarella*. Molecular and morphological evidence supports the placement of *Tauroprimnoa austasensis* within *Dasystenella* and *Fannyella kuekenthali* within *Metafannyella*.

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## 1. Introduction

## 1.1. Antarctic marine diversity

Evolution in Antarctica has been driven by a unique combination of plate tectonics, leading to the break-up of Gondwana, and an increasingly cold climate. The former began between 180 and 190 million years ago (MYA; e.g. Duncan et al., 1997; Encarnacion et al., 1996), and culminated in the physical isolation of the Antarctic continent by the Southern Ocean with the opening of the Drake Passage (~37–41 MYA; Scher and Martin, 2006) and the Tasman Seaway (~33 MYA; Kuhnt et al., 2004). Cooling of the Antarctic commenced in the Late Cretaceous but the onset of the Antarctic Circumpolar Current, and particularly its strengthening in the mid-Miocene, were events associated with marked decreases in ocean temperature (Sijp et al., 2014; Potter and Szatmari, 2009). The switch to orbitally-forced cycles of glaciations in the Neogene (e.g. Zachos et al., 2001) have further shaped the

evolution of Antarctic biota through advances and retreats of extensive ice sheets over the Antarctic continental shelf and slope (Thatje et al., 2005).

The unique tectonic and climatic history of the Antarctic has led to winners and losers amongst the marine biota (Rogers, 2012). Durophagous (shell-breaking) predators including cartilaginous and bony fishes and decapod crustaceans, along with groups showing other lifestyles, such as bivalve molluscs, are relatively poorly represented in the Southern Ocean and Antarctic coastal seas (Clarke and Crame, 2010). On the other hand, some animal groups have undergone conspicuous radiations. Most notable amongst these are the notothenioid fish, which are not only dominant in terms of numbers of species (101 of 222 Antarctic shelf and upper slope fish species; Eastman, 2005), but also in terms of their ecological importance (>90% abundance or biomass in Ross and Weddell Seas; Eastman, 2000, 2005; Ekau, 1990). Other groups in which there have been significant radiations include the peracarid Crustacea (Brandt, 2000; Lörz and Held, 2004), the pycnogonids (Clarke and Johnston, 2003), the Octopodidae (Allcock et al., 2011), and the liparid fish (Eastman, 1993).

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Why there has been such a lottery of success in the Antarctic marine biota has been subject to much speculation. For some taxa it has been suggested that there were specific physiological limitations to adapting to life in an environment characterised by extreme seasonality, cold and the presence of ice (e.g. [Frederich et al., 2001](#) for decapod crustaceans). However, other factors, including habitat loss (e.g. [Clarke and Crame, 2010](#)) and the lower rate of species origination at high latitudes (e.g. [Krug et al., 2009](#)), have also been put forward. Species radiations within the Antarctic may have been a partial response to the availability of niches vacated by intolerant taxa or the absence of ecological competitors or predators. Recent examination of fossil evidence from the Early Miocene Cape Melville Formation, on King George Island, indicate that community structure changed from one dominated by infaunal bivalves and decapod crustaceans to one more dominated by sessile suspension feeding species ([Whittle et al., 2014](#)). This is suggestive that the loss of durophagous predators from Antarctica may have been important in shaping the benthic communities observed today ([Whittle et al., 2014](#)). Ice sheet expansion and contraction driven by orbitally-forced cycles of glaciation may have also forced species up and down the continental slope or fragmented populations into glacial refugia thus promoting speciation (the so-called biodiversity pump hypothesis; [Clarke and Crame, 1992, 2010](#); [Thatje et al., 2005](#)). Movement up and down the slope may partially explain the eurybathy observed in many groups of animals ([Brandt et al., 2004, 2007](#)) and there is evidence of both emergence (e.g. *Benthoctopus*; [Strugnell et al., 2011](#)) and submergence (e.g. octopus; [Strugnell et al., 2008](#); isopods; [Raupach et al., 2009](#)) in the isothermal water column around Antarctica.

The current Antarctic marine benthic ecosystem comprises two core community types, one dominated by sessile suspension feeders and the other by mobile deposit feeders and infauna ([Gutt, 2007](#)). The former appears to be the more important community around the Antarctic continent although it varies substantially from place to place in terms of dominant species ([Gutt, 2007](#); [Gutt et al., 2013](#)). Sponges are the dominant organisms in many of these communities ([Gutt et al., 2013](#)) but bryozoans, cnidarians, ascidians and echinoderms are also important ([Griffiths et al., 2008](#); [Gutt, 2007](#); [Orejas et al., 2000](#)). Cnidarians, especially the octocorals, are conspicuous in adding to the three-dimensional structure of these communities ([Orejas et al., 2000](#)). Overall, the development of these communities is associated with strong currents providing a constant supply of suspended/resuspended particulate food. The great depth of the Antarctic shelf, ~450 m, a result of isostatic depression and past scouring by grounded ice sheets ([Clarke and Crame, 2010](#)), as well as a lack of terrigenous sediments because of low riverine inputs and thus estuaries and coastal mudflats, are also all favourable to the development of this community.

Here, we explore the evolution of Antarctic octocorals using the Family Primnoidae (Cnidaria: Octocorallia) as an example of one of the major suspension-feeding taxa in Antarctic benthic ecosystems. The Primnoidae have been described as the “quintessential deep-water octocoral family” ([Cairns and Bayer, 2009, p. 1](#)). Although the Primnoidae is a globally distributed, relatively common, deep-sea octocoral family, 23% of species have been sampled only within the sub-Antarctic. Colonies of this family can be very large, some *Primnoa* reaching 2 m in height and several metres in width ([Krieger and Wing, 2002](#)), making them important structural habitat for many associated species ([Krieger and Wing, 2002](#); [Metaxas and Davis, 2005](#)). Primnoids are believed to be most commonly found at bathyal-slope depths with few “shallower” (>200 m) occurrences of this family ([Griffiths et al., 2008](#); [Watling et al., 2011](#)). Many of the shallow-water Primnoidae occurrences are examples of “deep-water emergence” in fjords

where cooler waters support species usually only found in deep water (reviewed in [Waller et al., 2011](#)).

Primnoids, as with all deep-sea corals, are vulnerable to fisheries impacts ([Althaus et al., 2009](#); [Gianni, 2004](#); [Watling and Norse, 1998](#)); for example, they were the most common octocoral family in by-catch from longline fisheries for Patagonian toothfish around South Georgia ([Taylor, 2011](#)) and in the Ross Sea ([Parker and Bowden, 2010](#)). The deepest known alcyonacean is a Primnoidae, *Primnoella* (= *Convexella*) *krampi*, from the Kermadec Trench at 5850 m ([Madsen, 1956](#)). Primnoidae occur worldwide at depths of 8–5850 m.

Since the excellent, in depth, summary of the taxonomic history of Primnoidae by [Cairns and Bayer \(2009\)](#) there have been additional genus descriptions: *Tauroprimnoa* [= *Dasystemella*] and *Digitogorgia* ([Zapata-Guardiola and López-González, 2010a](#)), and *Scopaegorgia* ([Zapata-Guardiola and López-González, 2010b](#)). There have also been three genera revisions: *Amphilaphis* ([Zapata-Guardiola and López-González, 2012](#)); *Thouarella* ([Taylor et al., 2013a](#)); *Mirostenella* ([Zapata-Guardiola et al., 2013](#)), as well as a number of new species additions. There are currently 41 genera and 266 species within Primnoidae (see [Table 1](#)).

In this study we present an updated list of Primnoidae species and the first detailed phylogenetic analysis of Primnoidae. We specifically examine the timing of radiation seen within sub-Antarctic Primnoidae to see whether it coincides, as with other groups, with major tectonic and climatic events ([Rogers, 2012](#)). This analysis also casts light on whether Antarctic primnoids are a result of polar emergence or whether the Antarctic has acted as a centre of speciation/origin for this “deep-sea” family (e.g. octopus; [Strugnell et al., 2008](#)).

## 2. Materials and methods

### 2.1. Samples

Samples were obtained from a range of sources, mostly museums (MNHN – Muséum National d’Histoire Naturelle, Paris; Smithsonian Institution, Washington DC), expeditions (R/V *James Cook* JC66, R/V *Nathanial B. Palmer* 11-03), and university collections (author collection, stored at the University of Oxford; Atlantis Project, IEO – Centro Oceanográfico de Gijón, Spain). Expedition samples were stored in 95% ethanol and the authors’ collections in 70% ethanol (with genetics samples in 95%). The history of sample preservation from museum specimens was hard to verify given many were originally preserved at the turn of the 20th century. In total 39 of the known 41 genera of Primnoidae were sourced ([Table 1](#)). Of these 39 genera it was possible to extract and amplify DNA for 25 genera. The most common reason for unsuccessful DNA amplification was likely sample age.

To place the Primnoidae within a wider context, specimens from GenBank were included but only if 2 or more relevant genes were available from the same specimen. Eight specimens were added to the analysis this way. In total 25 genera are represented including 64 species.

### 2.2. DNA extraction and amplification

Extraction elutions of 50 µl were undertaken using Qiagen Blood and Tissue Kit (Qiagen Ltd. Crawley, East Sussex, UK). Five gene regions were targeted: *cox1*, mtMutS (often written in octocoral research as *msh1* however the name mtMutS makes fewer assumptions about gene origins; [Bilewitch and Degnan, 2011](#)), 16S, 18S and 28S. PCR reactions were conducted using 8 µl of Master mix with HotStarTaq (Qiagen), 2 µl template DNA and 1 µl of each primer (2 µM): total volume 12 µl. PCR conditions

**Table 1**

A list of current, valid, genera and species within Primnoidae, including the synonymisation of *Tauroprimnoa* with *Dasystenella*, and new combination of *Metafannyella kuekenthalii*, described herein (modified from Cairns and Bayer, 2009).

Genus	Ordered by age of genus description	Genus range	Genus depth range (m)	Year genus instated	Year species instated	Holotype locality/ Known species range
<i>Acanthoprimnoa</i> Cairns and Bayer, 2004	* <i>A. goesi</i> (Aurivillius, 1931)	Caribbean, Japan	45–686	2004	1931	Florida and Caribbean
	<i>A. cristata</i> (Kükenthal and Gorzawsky, 1908) = <i>P. carinata</i> Kinoshita, 1908					
<i>Aglaoprimnoa</i> Bayer, 1996	<i>A. sarta typica</i> (Kükenthal and Gorzawsky, 1908) – <i>A. s. squamosa</i> (Kükenthal and Gorzawsky, 1908)	Sub-Antarctic to S. America	70–686	1996	1908	Japan
	<i>A. pectinata</i> Cairns and Bayer, 2004 * <i>A. stefanii</i> Bayer, 1996					
<i>Ainigmaptilon</i> Dean, 1926 (= <i>Lycurus</i> Molander, 1929)	* <i>A. haswelli</i> Dean, 1926	Antarctica to South Georgia	75–817	1926	1926	Antarctica, South Georgia
	<i>A. antarcticum</i> (Molander, 1929)					
	<i>A. virgularoides</i> (Molander, 1929)					
	<i>A. wallini</i> Carlgren, 1943					
<i>Armadillologorgia</i> Bayer, 1980	<i>A. edisto</i> Bayer, 1950	South Georgia, Scotia Sea	659–1886	1980	1980	South Georgia, west Antarctic peninsula
	* <i>A. cyathella</i> Bayer, 1980					
<i>Arntzia</i> López-González, Gili and Orejas, 2002	<i>A. albertoi</i> Cerino and Lauretta, 2013	Antarctica	200–3447	2002	2013	Argentina
	* <i>A. gracilis</i> (Molander, 1929)					
<i>Arthrogorgia</i> Kükenthal in Kükenthal and Gorzawsky, 1908	* <i>A. ijimai</i> (Kinoshita, 1907)	North Pacific	163–1127	1908	1907	Japan
	= <i>A. membranacea</i> Kükenthal and Gorzawsky, 1908a <i>A. kinoshitai</i> Bayer, 1952					
<i>Australogorgia</i> Cairns and Bayer 2009	<i>A. otsukai</i> Bayer, 1952	Off Tasmania	1200	2009	1952	Aleutian Islands to Alaska
	<i>A. utinomii</i> Bayer, 1996					
<i>Callogorgia</i> Gray, 1858 (= <i>Xiphocella</i> Gray, 1870; = <i>Callicella</i> Gray, 1870; = <i>Caligorgia</i> sensu Wright and Studer, 1889: spelling variation)	* <i>A. aldersladei</i> Cairns and Bayer 2009	Indo-Pacific, N. Atlantic	37–2472	1858	1766	E. Atlantic, Mediterranean
	* <i>C. verticillata</i> (Pallas, 1766)					
<i>Callogorgia</i> Gray, 1858 (= <i>Xiphocella</i> Gray, 1870; = <i>Callicella</i> Gray, 1870; = <i>Caligorgia</i> sensu Wright and Studer, 1889: spelling variation)	– <i>C. v. var. grimaldii</i> (Studer, 1890)					
	<i>C. flabellum typica</i> (Ehrenberg, 1834) = <i>Primnoa flabellum</i> Ehrenberg, 1834					
	– <i>C. f. grandis</i> Kükenthal and Gorzawsky, 1908a					
	<i>C. elegans</i> (Gray, 1870)					
	<i>C. ventilabrum</i> (Studer, 1878)					
	<i>C. modesta</i> (Studer, 1879)					
	<i>C. sertosa</i> (Wright and Studer, 1889)					
	<i>C. gracilis</i> (Milne Edwards and Haime, 1857)					
	<i>C. versluysi</i> (Thomson, 1905)					
	<i>C. dubia</i> (Thomson and Henderson, 1906)					
	<i>C. indica</i> Versluys, 1906					
	<i>C. robusta</i> (Versluys, 1906)					
	<i>C. joubini</i> (Versluys, 1906)					
	<i>C. pennacea</i> (Versluys, 1906)					
	<i>C. minuta</i> (Versluys, 1906)					
	<i>C. affinis</i> (Versluys, 1906)					
	<i>C. similis</i> (Versluys, 1906)					
	<i>C. formosa</i> Kükenthal, 1907					
	= <i>Primnoella indica</i> Kükenthal, 1907 (junior secondary homonym: <i>P. indica</i> Verrill, 1906)					

(continued on next page)

Table 1 (continued)

Genus	Ordered by age of genus description	Genus range	Genus depth range (m)	Year genus instated	Year species instated	Holotype locality/ Known species range	
<i>Callozostron</i> Wright, 1885	<i>C. gilberti</i> (Nutting, 1908)				1908	Hawaii to NW Atlantic	
	<i>C. ramosa</i> (Kükenthal and Gorzawsky, 1908a)				1908	central Indo-Pacific	
	<i>C. laevis</i> (Thomson and Mackinnon, 1911)				1911	Australia	
	<i>C. kinoshitae</i> Kükenthal, 1913				1913	California	
	<i>C. cristata</i> Aurivillius, 1931				1931	Japan	
	= <i>C. weltneri</i> (Versluys, 1906)						
	<i>C. chariessa</i> Bayer, 1982					1982	Philippines
	<i>C. linguimaris</i> Cairns and Bayer, 2002					2002	Bahamas
	<i>C. americana americana</i> Cairns and Bayer, 2002					2002	Caribbean to Florida
	– <i>C. a. delta</i> Cairns and Bayer, 2002					2002	
	* <i>C. mirabile</i> Wright, 1885	Antarctic, New Zealand		1354–3876	1885	1885	Antarctica, New Zealand
	= <i>C. horridum</i> Kükenthal, 1909						
	<i>C. carlottae</i> Kükenthal, 1909					1909	Antarctica
<i>C. acanthodes</i> Bayer, 1996					1996	South Georgia, sub-Antarctic	
<i>Calyptrophora</i> Gray, 1866	<i>C. diplodiadema</i> Bayer, 1996					1996	New Zealand
	<i>japonica</i> complex	Pacific, W. Atlantic	229–3107	1866			
	“Species group 1” (sensu Bayer, 2001)					2001	
	* <i>C. japonica</i> Gray, 1866					1866	Japan, west Pacific
	– form A Versluys, 1906					1906	
	<i>C. clarki</i> Bayer, 1951					1951	Hawaii
	= <i>C. japonica</i> form B Versluys, 1906						
	= <i>C. japonica</i> Nutting, 1908						
	<i>C. juliae</i> Bayer, 1952					1952	Philippines
	<i>C. spinosa</i> Pasternak, 1984					1984	Micronesia, central Indo-Pacific
	<i>C. microdentata</i> Pasternak, 1985					1985	NW to W. Atlantic & Caribbean
	= <i>C. pillsburyae</i> Bayer, 2001						
	<i>C. gerdae</i> Bayer, 2001					2001	Florida to Bahamas
	<i>C. antilla</i> Bayer, 2001					2001	Caribbean
	<i>C. clinata</i> Cairns, 2007a					2007	NW Atlantic
	<i>C. bayeri</i> Cairns, 2007b					2007	NE Pacific
	<i>C. laevispinosa</i> Cairns, 2007b					2007	NE Pacific
	<i>C. pileata</i> Cairns 2009					2009	Hawaii, W. Pacific
	– <i>C. japonica</i> form C Versluys, 1906						
	<i>C. alpha</i> Cairns 2009					2009	Hawaii
	<i>C. cucullata</i> Cairns, 2012					2012	New Zealand
	<i>C. cristata</i> Cairns, 2012					2012	New Zealand
	“Species group 2” (sensu Bayer, 2001)					2001	
<i>C. trilepis</i> (Pourtaes, 1868)					1868	Blake Plateau, Florida, Cuba	
<i>C. angularis</i> (Nutting, 1908)					1908	Hawaii	
<i>C. inornata</i> Cairns, 2012					2012	New Zealand, New Caledonia	
<i>C. niwa</i> Cairns, 2012					2012		
<i>wyvillei</i> complex							
<i>C. wyvillei</i> Wright, 1885					1885	Hawaii, New Zealand	
<i>C. agassizii</i> Studer, 1894					1894	Galapagos, east Pacific	
= <i>C. versluysi</i> Nutting, 1908							
<i>C. clinata</i> Cairns, 2012					2012	N. Atlantic, New Zealand	
<i>C. diaphana</i> Cairns, 2012					2012	New Zealand	

<i>Candidella</i> Bayer, 1954 (nomen novum for <i>Stenella</i> Gray, 1870, not Gray, 1866)	* <i>C. imbricata</i> (Johnson, 1862)	Atlantic, central Pacific	378–2165	1854	1862	North Atlantic
	<i>C. johnsoni</i> (Wright and Studer, 1889)				1889	Ascension Island, S. mid-Atlantic
	<i>C. gigantea</i> (Wright and Studer, 1889)				1889	Fiji, NW Hawaii, Atlantic
	<i>C. helminthophora</i> (Nutting, 1908)				1908	Hawaii
<i>Convexella</i> Bayer, 1996	* <i>C. magelhaenica</i> (Studer, 1879)	Antarctic, Kermadec, North Atlantic	12–5850	1996	1879	Atlantic sub-Antarctic
	= <i>Primnoella flagellum</i> Studer, 1878					
	=? <i>P. vanhoeffeni</i> Kükenthal, 1909					
	= <i>C. murrayi</i> (Wright and Studer, 1889)					
	<i>C. divergens</i> (Hickson, 1907)				1907	Antarctica
	<i>C. jungerseni</i> (Madsen, 1944)				1944	N. Atlantic
	<i>C. krampi</i> (Madsen, 1956)				1956	W. Pacific
<i>Dasystenella</i> Versluys, 1906	* <i>D. acanthina</i> (Wright and Studer, 1889)	Sub-Antarctic South Atlantic	300–5087	1906	1889	Shetland Islands, Scotia Ridge
	= <i>Thouarella longispinosa</i> (Kükenthal, 1912)					
	– <i>T. h. forma plumatilis</i> Aurivillius, 1931				1931	
	= <i>Tauroprimnoa austasensis</i> (Zapata-Guardiola and López-González, 2010)					
<i>Digitogorgia</i> Zapata-Guardiola and López-González, 2010	* <i>D. kuekenhali</i> Zapata-Guardiola and López-González, 2010	Sub-Antarctic	286.3–2259	2010	2010	Argentina to Scotia Sea
	<i>D. brochii</i> Zapata-Guardiola and López-González, 2010				2010	Burdwood Bank
<i>Fanellia</i> Gray, 1870	* <i>F. compressa</i> (Verrill, 1865)	West, central, & N. Pacific	92–1028	1870	1865	Aleutian Islands, Bering Sea
	<i>F. tuberculata</i> (Versluys, 1906)				1906	Philippines, New Caledonia, Hawaii
	= <i>Caligorgia aspera</i> Kinoshita, 1908					
	= <i>C. pseudoflabellum</i> Bayer, 1949					
	<i>F. granulosa</i> (Kinoshita, 1907)				1907	Japan, Vanuatu
	<i>F. fraseri</i> (Hickson, 1915)				1915	Gulf of Alaska
	<i>F. corymbosa</i> Bayer, 1982				1982	Indonesia
	<i>F. medialis</i> Bayer and Stefani, 1989				1989	Hawaii, Society Islands, Madagascar
	<i>F. euthyeia</i> Bayer and Stefani, 1989				1989	Hawaii, Society Islands, New Caledonia
	<i>F. korema</i> Bayer and Stefani, 1989				1989	New Caledonia, Solomon Islands
<i>Fannyella</i> ( <i>Fannyella</i> ) ss. Gray, 1872 (= <i>Ascolepis</i> Thomson and Rennet, 1931)	* <i>F. rossii</i> Gray, 1872	Antarctic	46–852	1872	1872	circum-Antarctic
	=? <i>Caligorgia antarctica</i> Kükenthal, 1909					
	= <i>Ascolepis splendens</i> Thomson and Rennet, 1931					
<i>Fannyella</i> ( <i>Scyphogorgia</i> ), Cairns and Bayer 2009	* <i>F. abies</i> (Broch, 1965)	Antarctic	94–550	2009	1965	sub-Antarctic
	= <i>Thouarella abies</i> Broch, 1965					
<i>Fannyella</i> ( <i>Cyathogorgia</i> ), Cairns and Bayer 2009	* <i>F. spinosa</i> (Thomson and Rennet, 1931)	Antarctic	55–485	2009	1931	circum-Antarctic
	– <i>F. spinosa</i> "intermediate form" Bayer, 1998				1998	
<i>Helicoprinoea</i> Cairns, 2012	* <i>H. fasciola</i> Cairns, 2012	New Zealand	138	2012	2012	New Zealand
<i>Heptaprinoea</i> Cairns, 2012	* <i>H. patagonica</i> Cairns, 2012	sub-Antarctic	265–1248	2012	2012	Argentina, Burdwood Bank, sub-Antarctic
<i>Metanarella</i> Cairns, 2012	* <i>M. nannolepis</i> Cairns, 2012	New Zealand	138–168	2012	2012	New Zealand
<i>Microprimnoa</i> Bayer and Stefani, 1989	* <i>M. diabathra</i> Bayer and Stefani, 1989	New Caledonia	415	1989	1989	New Caledonia
<i>Mirostenella</i> Bayer, 1988	* <i>M. articulata</i> Bayer, 1988	Sub-Antarctic	201–1647	1988	1988	South Georgia, sub-Antarctic

(continued on next page)

Table 1 (continued)

Genus	Ordered by age of genus description	Genus range	Genus depth range (m)	Year genus instated	Year species instated	Holotype locality/ Known species range	
<i>Narella</i> Gray, 1870 (= <i>Stachyodes</i> Wright and Studer in Studer, 1887; not <i>Stachyodes</i> Bargatzky, 1881 (a stromatoporoid); = <i>Calypterinus</i> Wright and Studer in Studer, 1887)	* <i>N. regularis</i> (Duchassaing and Michelotti, 1860)	Cosmopolitan	55–4594	1870	1860	Caribbean	
	<i>N. allmani</i> (Wright and Studer, 1889)						
	<i>N. ambigua</i> (Studer, 1894)				1894	E. Pacific, Galapagos	
	<i>N. clavata</i> (Versluys, 1906)				1906	Indonesia, Philippines	
	<i>N. horrida</i> (Versluys, 1906)				1906	Indonesia	
	<i>N. obscura</i> (Versluys, 1906)				1906	Indonesia	
	<i>N. orientalis</i> (Versluys, 1906)				1906	Indonesia	
	<i>N. parva</i> (Versluys, 1906)				1906	Indonesia, Philippines	
	<i>N. dichotoma</i> (Versluys, 1906)				1906	W. Pacific	
	= <i>N. nuttingi</i> Bayer, 1997						
	<i>N. studeri</i> (Versluys, 1906:94) (nomen novum for <i>S. regularis</i> Wright and Studer, 1889)					1906	central Indo-Pacific
	<i>N. grandiflora</i> (Kükenthal, 1907)					1907	Indonesia
	<i>N. biannulata</i> (Kinoshita, 1907)					1907	Japan
	<i>N. irregularis</i> (Kinoshita, 1907)					1907	Japan
	<i>N. megalepis</i> (Kinoshita, 1908)					1908	Japan
	<i>N. compressa</i> (Kinoshita, 1908)					1908	Japan
	<i>N. bowersi</i> (Nutting, 1908)					1908	E. Pacific
	<i>N. versluysi</i> (Hickson, 1909)					1909	Amphi-Atlantic
	=? <i>N. elegans</i> Tixier-Durivault and Lafargue, 1968						
	<i>N. gilchristi</i> (Thomson, 1911)					1911	SW Indian Ocean
	= <i>S. capensis</i> Thomson, 1917						
	= <i>Stachyodes "gilberti"</i> Kükenthal, 1919 (mis-spelling of <i>gilchristi</i> )						
	<i>N. gaussi</i> (Kükenthal, 1912)					1912	Antarctica
	<i>N. bellissima</i> (Kükenthal, 1915)					1915	Amphi-Atlantic
	<i>N. japonensis</i> (Aurivillius, 1931)					1931	Japan
	<i>N. laxa</i> Deichmann, 1936					1936	NW Atlantic
	<i>N. pauciflora</i> Deichmann, 1936					1936	Caribbean
	<i>N. leilae</i> Bayer, 1951					1951	Indonesia
	<i>N. ornata</i> Bayer, 1995					1995	Hawaii
	<i>N. spectabilis</i> Cairns and Bayer, 2003					2003	Bahamas
	<i>N. alvinae</i> Cairns and Bayer, 2003					2003	Bermuda
	<i>N. bayeri</i> Cairns and Baco, 2007					2007	Gulf of Alaska
	<i>N. arbuscula</i> Cairns and Baco, 2007					2007	Gulf of Alaska
	<i>N. cristata</i> Cairns and Baco, 2007					2007	Gulf of Alaska
	<i>N. abyssalis</i> Cairns and Baco, 2007					2007	Gulf of Alaska
	<i>N. alaskensis</i> Cairns and Baco, 2007					2007	Gulf of Alaska
	<i>N. hawaiiensis</i> Cairns and Bayer, 2008					2007	Hawaii
	<i>N. gigas</i> Cairns and Bayer, 2008					2007	Hawaii
	<i>N. muzikae</i> Cairns and Bayer, 2008					2007	Hawaii
	<i>N. vermifera</i> Cairns and Bayer, 2008					2007	Hawaii
<i>N. macrocalyx</i> Cairns and Bayer, 2008					2007	Hawaii	
<i>N. alata</i> Cairns and Bayer, 2008					2007	Hawaii	
<i>N. mesolepis</i> Cairns, 2012					2012	New Zealand	
<i>N. hypsocalyx</i> Cairns, 2012					2012	New Zealand	
<i>N. vulgaris</i> Cairns, 2012					2012	New Zealand	
<i>N. mosaica</i> Cairns, 2012					2012	New Zealand	
<i>N. dampieri</i> Cairns, 2012					2012	New Zealand	
<i>Narelloides</i> Cairns, 2012		New Zealand	157–224	2012	2012	New Zealand	
<i>Onogorgia</i> , Cairns and Bayer 2009	* <i>N. crinitus</i> Cairns, 2012	Antarctic	22–433	2009	1929	sub-Antarctic	
	* <i>O. nodosa</i> (Molander, 1929)						
	= <i>Primnoella vanhoefeni</i> sensu Kükenthal, 1912						
<i>Ophidiogorgia</i> Bayer, 1980	* <i>O. paradoxa</i> Bayer, 1980	Antarctica	27–426	1980	1980	circum-Antarctic	
	<i>O. kuekenthali</i> (Gravier, 1913)				1913	circum-Antarctic	

<i>Paracalyptophora</i> Kinoshita, 1908	* <i>P. kerberti</i> (Versluys, 1906)	Western and central Pacific, North Atlantic	150–1480	1908	1906	Japan
	<i>P. josephinae</i> (Lindström, 1877)				1877	E. Atlantic
	<i>P. mariae</i> (Versluys, 1906)				1906	S. Pacific
	<i>P. duplex</i> Cairns and Bayer, 2004				2004	Florida to Cuba
	<i>P. simplex</i> Cairns and Bayer, 2004				2004	Florida, USA
	<i>P. carinata</i> Cairns and Bayer, 2004				2004	Caribbean
	<i>P. echinata</i> Cairns 2009				2009	Hawaii
	<i>P. hawaiiensis</i> Cairns 2009				2009	Hawaii
<i>Paranarella</i> Cairns, 2007	* <i>P. watlingi</i> Cairns, 2007	NW Atlantic	3855	2007	2007	NW Atlantic
<i>Metafammyella</i> Cairns and Bayer 2009	* <i>M. lepidota</i> (Bayer, 1998)	Antarctic	265–1280	2009	1998	Antarctica
	<i>M. eos</i> (Bayer, 1998)				1998	S. Pacific
	<i>M. aurora</i> (Bayer, 1998)				1998	Antarctic peninsula
	<i>M. mawsoni</i> (Bayer, 1998)				1998	Antarctica
	<i>M. kuekenthali</i> (Molander, 1929) new combination				1929	sub-Antarctic
<i>Parastenella</i> Versluys, 1906	* <i>P. doederleini</i> (Wright and Studer, 1889)	Cosmopolitan, except east Atlantic	567–3470	1906	1889	Aleutian Islands to Alaska
	<i>P. spinosa</i> (Wright and Studer, 1889)				1889	South Georgia, south Indian Ocean
	<i>P. ramosa</i> (Studer, 1894)				1894	Aleutian Islands to Alaska
	<i>P. atlantica</i> Cairns, 2007				2007	NW Atlantic
	<i>P. gymnogaster</i> Cairns, 2007				2007	Aleutian Islands to Alaska
	<i>P. pacifica</i> Cairns, 2007				2007	Oregon, British Columbia, USA
	<i>P. bayeri</i> Cairns 2010				2010	Hawaii
<i>Perissogorgia</i> Bayer and Stefani, 1989	* <i>P. viridis</i> Bayer and Stefani, 1989	New Caledonia	55–750	1989	1989	New Caledonia
	<i>P. petasus</i> Bayer and Stefani, 1989				1989	New Caledonia
	<i>P. colossus</i> Bayer and Stefani, 1989				1989	New Zealand, New Caledonia
	<i>P. bythia</i> Bayer and Stefani, 1989				1989	New Caledonia
	<i>P. vitrea</i> Bayer and Stefani, 1989				1989	New Caledonia
	<i>P. monile</i> Bayer and Stefani, 1989				1989	New Caledonia
	<i>P. penna</i> Bayer and Stefani, 1989				1989	New Caledonia
<i>Plumarella</i> ( <i>Plumarella</i> ) Gray, 1870	* <i>P. penna</i> (Lamarck, 1815)	W. Pacific, Patagonia, NW Atlantic	10–1914	1870	1815	Australia
	<i>P. pourtalesii</i> (Verrill, 1883)				1883	W. Atlantic to Cuba
	– <i>P. p.</i> forma <i>robusta</i> Deichmann, 1936					
	– <i>P. p.</i> forma <i>obtusa</i> Cairns and Bayer, 2004					
	<i>P. delicatissima</i> Wright and Studer, 1889				1889	
	<i>P. flabellata</i> Versluys, 1906				1906	
	<i>P. spinosa typica</i> Kinoshita, 1907				1907	
	– <i>P. s. brevispina</i> Kükenthal, 1919					
	<i>P. alba</i> Kinoshita, 1908				1908	
	<i>P. gracilis</i> Kinoshita, 1908				1908	
	<i>P. longispina</i> Kinoshita, 1908				1908	
	<i>P. acuminata</i> Kinoshita, 1908				1908	
	<i>P. dofleini</i> Kükenthal and Gorzawsky, 1908				1908	
	– <i>P. d.</i> var. <i>boninensis</i> Aurivillius, 1931					
	<i>P. lata</i> Kükenthal and Gorzawsky, 1908				1908	
	<i>P. rigida</i> Kükenthal and Gorzawsky, 1908				1908	
	<i>P. dentata</i> Thomson and Russell, 1910				1910	
	<i>P. laevis</i> Thomson and Mackinnon, 1911				1911	
	<i>P. adhaerans</i> Nutting, 1912				1912	
	<i>P. recta</i> (Nutting, 1912)				1912	Japan

(continued on next page)

Table 1 (continued)

Genus	Ordered by age of genus description	Genus range	Genus depth range (m)	Year genus instated	Year species instated	Holotype locality/ Known species range
	= <i>P. alternata</i> (Nutting, 1912) = <i>P. attenuata</i> Kükenthal, 301:1924 (misspelling of <i>alternata</i> ) <i>P. spicata</i> Nutting, 1912 <i>P. aurea</i> (Deichmann, 1936) <i>P. pellucida</i> Cairns and Bayer, 2004				1912 1936 2004	Alaska, Bering Sea S. Carolina to Cuba NW Atlantic to Bahamas
	<i>P. laxiramosa</i> Cairns and Bayer, 2004 <i>P. dichotoma</i> Cairns and Bayer, 2004				2004 2004	N and S Carolina, USA S. Carolina to Florida, USA
	<i>P. aculeata</i> Cairns and Bayer, 2004 <i>P. diadema</i> (Cairns, 2006)				2004 2006	Bahamas Brazil to South Georgia, sub-Antarctic
	<i>P. circumperculum</i> Cairns, 2010 <i>P. undulata</i> (Zapata-Guardiola and López-González, 2010)				2010 2010	Hawaii W. Atlantic - Brazil to Argentina, South Georgia
	= <i>Thouarella sardana</i> Zapata-Guardiola and López-González, 2010 <i>P. bayeri</i> (Zapata-Guardiola and López-González, 2010)				2010 2010	South Georgia, sub-Antarctic
<i>Plumarella</i> ( <i>Dicholaphis</i> ) Kinoshita, 1907	* <i>P. delicata</i> Kinoshita, 1907 <i>P. superba</i> (Nutting, 1912) <i>P. profunda</i> Cairns 2011 <i>P. hapala</i> Cairns 2011 <i>P. aleutiana</i> Cairns 2011 <i>P. nuttingi</i> Cairns 2011 <i>P. echinata</i> Cairns 2011 <i>P. robusta</i> Cairns 2011	Off Japan	731	1907	1907 1912 2011 2011 2011 2011 2011	Japan Aleutian Islands Alaska Alaska, Bering Sea Alaska Alaska, Bering Sea Alaska
<i>Plumarella</i> ( <i>Faxiella</i> ) Zapata-Guardiola and López-González, 2012	* <i>P. abietina</i> (Studer, 1894)	W. USA to Galapagos	3181	2013	1894	central America to Galapagos
	<i>P. delicatula</i> (Thomson and Rennet, 1931)				1931	Macquarie Island, sub-Antarctic
<i>Plumarella</i> ( <i>Verticillata</i> ) Zapata-Guardiola, López-González, and Gili, 2013	* <i>P. castellivae</i> Zapata-Guardiola, López-González, and Gili, 2013	Sub-Antarctic	120–2044	2013	2013	sub-Antarctic: Argentina to Scotia Sea
<i>Primnoa</i> Lamouroux, 1812	<i>P. resedaeformis typica</i> (Gunnerus, 1763)	N. Atlantic, N. Pacific, sub-Antarctic	9–1020	1812	1763	N. Atlantic, Arctic, N. Pacific
	= <i>Gorgonia reseda</i> Pallas, 1766 =* <i>Gorgonia lepadifera</i> Linnaeus, 1767 <i>P. pacifica</i> Kinoshita, 1907				1766 1907	
	– <i>P. pacifica</i> var. <i>willeyi</i> (Hickson, 1915) Not + <i>P. costata</i> Nielsen, 1913 (Early Paleocene, Denmark) Not + <i>P. gracilis</i> Nielsen, 1925 (= <i>Eiphaxum auloporoides</i> (Lonsdale, 1850) Early Paleocene, Denmark)				1915 1913 1925	
	<i>P. notialis</i> Cairns and Bayer, 2005 <i>P. wingi</i> Cairns and Bayer, 2005				2005 2005	sub-Antarctic Aleutian Islands
<i>Primnocapsa</i> Zapata-Guardiola and López-González, 2012	* <i>P. plumacea</i> Thomson and Mackinnon, 1911	Australia	54.6–73.12	2012	1911	Australia
<i>Primnoeides</i> Studer and Wright in Studer, 1887	* <i>P. sertularoides</i> Wright and Studer, 1889	S. Indian Ocean	400–558	1887	1889	South Africa to SW Indian Ocean
<i>Primnoella</i> Gray, 1858 (= <i>Callirhabdos</i> Philippi, 1894)	* <i>P. australasiae</i> (Gray, 1850)	W. Atlantic, Australia, New Zealand	8–1249	1858	1850	Australia, Tasmania, New Zealand



		Zealand							
	<i>P. divaricata</i> (Studer, 1879)							1879	Uruguay, Argentina
	<i>P. distans</i> Studer, 1879							1879	West Indies, off Pernambuco
	<i>P. grandisquamis</i> Wright and Studer, 1889							1889	Australia
	<i>P. chilensis</i> (Philippi, 1894)							1894	Patagonia, Chile, South Georgia
	= <i>P. philippii</i> Aurivillius, 1931								
	= <i>P. biserialis</i> Wright and Studer, 1889								
	<i>P. scotiae</i> Thomson and Richie, 1906							1906	Burdwood Bank, South Georgia
	= <i>P. compressa</i> Kükenthal, 1908								
	? <i>P. antarctica</i> Kükenthal, 1907							1907	Bouvet Island, sub- Antarctic
	<i>P. delicatissima</i> Kükenthal, 1909							1909	Off Rio de Janeiro and Amapa Brazil
	<i>P. laevis</i> (Thomson and Mackinnon, 1911)							1911	SW Australia
	<i>P. polita</i> Deichmann, 1936							1936	Caribbean
<i>Pterostenella</i> Versluys, 1906	* <i>P. plumatilis</i> (Milne Edwards, 1857)	Indo-western Pacific	60–75	1906				1857	Indo-west Pacific
	<i>P. anatole</i> Bayer and Stefani, 1989							1989	New Caledonia
<i>Pseudoplumarella</i> Kükenthal, 1915	* <i>P. thetis</i> (Thomson and MacKinnon, 1911)	E. Australia	55–115	1915				1911	New South Wales, Australia
	<i>P. corruscans</i> (Thomson and Mackinnon, 1911)							1911	New South Wales, Australia
	<i>P. filicoides</i> (Thomson and Mackinnon, 1911)							1911	New South Wales, Australia
	<i>P. versluysi</i> (Thomson and Mackinnon, 1911)							1911	New South Wales, Australia
	<i>P. echidna</i> Bayer, 1981							1981	E. Australia
<i>Pyrogorgia</i> , Cairns and Bayer 2009	* <i>P. lemnos</i> (Bayer, 1998)	Tierra del Fuego	384–511	2009				1998	Argentina to Antarctica
<i>Scopaegorgia</i> , Zapata-Guardiola and López-González, 2010	* <i>S. liouvillei</i> (Gravier, 1913)	Antarctica	151.3– 597.6	2010				1913	Antarctica
	= <i>Stenella</i> ( <i>Dasystenella</i> ) <i>liouvillei</i> (Gravier, 1913)								
<i>Thouarella</i> ( <i>Thouarella</i> ) Gray, 1870 (= <i>Rhopalonella</i> Roule, 1908;	* <i>T. antarctica</i> (Valenciennes, 1846)	Sub-Antarctic, W. Atlantic, N. Pacific	60–1644	1870				1846	Falkland Islands, SW Atlantic
<i>Thouarella</i> ( <i>Euthouarella</i> ) Kükenthal, 1915	<i>T. hilgendorfi</i> (Studer, 1878)							1878	Hawaii, Indonesia, Indian Ocean, Japan
= <i>Primnodendron</i> Nutting, 1912; = <i>Parathouarella</i> Kükenthal, 1915)	= <i>T. typica</i> Kinoshita, 1907							1907	
	<i>T. variabilis typica</i> Wright and Studer, 1889							1889	Circum-Antarctic
	– var. <i>brevispinosa</i> Wright and Studer, 1889							1889	
	– var. <i>gracilis</i> Wright and Studer, 1889							1889	
	<i>T. koellikeri</i> Wright and Studer, 1889							1889	SE Pacific, SW Atlantic, Antarctic Peninsula
	<i>T. moseleyi</i> Wright and Studer, 1889							1889	New Zealand and Indonesia
	<i>T. affinis</i> Wright and Studer, 1889							1889	SW to S. Atlantic
	<i>T. regularis</i> (Wright and Studer, 1889)							1889	S. Atlantic, sub- Antarctic
	<i>T. brucei</i> (Thomson and Richie, 1906)							1906	S. Atlantic, SE Pacific, Antarctic Peninsula
	= <i>T. versluysi</i> Kükenthal, 1907							1907	
	<i>T. laxa</i> Versluys, 1906							1906	E. Africa to central Indo-Pacific

(continued on next page)

Table 1 (continued)

Genus	Ordered by age of genus description	Genus range	Genus depth range (m)	Year genus instated	Year species instated	Holotype locality/ Known species range
	= <i>T. tenuisquamis</i> Kükenthal, 1908				1908	
	= <i>T. flabellata</i> Kükenthal, 1907				1907	
	= <i>T. carinata</i> Kükenthal, 1908				1908	
	<i>T. tydemani</i> Versluys, 1906				1906	Indonesia
	=? <i>Hookerella pulchella</i> Gray, 1870					
	<i>T. striata</i> Kükenthal, 1907				1907	Bouvet Island, SW Atlantic, Patagonian shelf
	<i>T. crenelata</i> Kükenthal, 1907				1907	Circum sub-Antarctic
	<i>T. pendulina</i> (Roule, 1908)				1908	Circum-Antarctic, S. Atlantic, S. Indian Ocean
	<i>T. clavata</i> Kükenthal, 1908				1908	South Africa
	<i>T. coronata</i> Kinoshita, 1908				1908	Japan
	<i>T. parva</i> Kinoshita, 1908				1908	Japan
	<i>T. chilensis</i> Kükenthal, 1908				1908	Circum-Antarctic, S Atlantic, S Indian Ocean
	<i>T. biserialis</i> (Nutting, 1908)				1908	Hawaii
	= <i>Amphilaphis biserialis</i> (Nutting, 1908)					
	<i>T. hicksoni</i> Thomson, 1911				1911	South Africa
	<i>T. dispersa</i> (Kükenthal, 1912)				1912	Antarctica
	<i>T. grandiflora</i> (Kükenthal, 1912)				1912	Antarctica
	<i>T. bipinnata</i> Cairns, 2006				2006	Central W Atlantic
	<i>T. grasshoffi</i> Cairns, 2006				2006	N. Atlantic
	<i>T. viridis</i> Zapata-Guardiola and López-González, 2010				2010	South Georgia, Patagonian shelf
	<i>T. minuta</i> Zapata-Guardiola and López-González, 2010				2010	Circum-Antarctic
	<i>T. andeep</i> Zapata-Guardiola and López-González, 2010				2010	Circum-Antarctic, SW Atlantic
	<i>T. parachilensis</i> Taylor, et al., 2013				2013	South Georgia, Antarctic peninsula
	<i>T. cristata</i> Cairns 2011				2011	Alaska, Bering Sea
	<i>T. trilineata</i> Cairns 2011				2011	Alaska
	<i>T. vitjaz</i> Zapata-Guardiola and López-González, 2013				2013	N. Pacific, Hawaii
Tokoprymno Bayer, 1996	* <i>T. maia</i> Bayer, 1996	Sub-antarctic	549–2896.4	1996	1996	sub-Antarctic Pacific
	<i>T. anatis</i> Zapata-Guardiola and López-González, 2010				2010	South Georgia, Antarctic peninsula

Type species are marked with an asterisk and listed first, other species are chronological thereafter. + indicates a fossil species. A dash precedes a form, variety or subspecies.

**Table 2**  
Alignment information.

Gene and position (1st, 2nd, or 3rd)	Data without Gblocks			Data with Gblocks		
	Partition number	Partition delineation	Best-fit model of evolution	Partition number	Partition delineation	Best-fit model of evolution
cox1 – 1st	1	1-816/3	GTR + I + G	1	1-579/3	HKY + I + G
cox1 – 2nd	2	2-816/3	HKY + I + G	2	2-579/3	F81
cox1 – 3rd	3	3-816/3	GTR + G	3	3-579/3	GTR + G
mtMutS – 1st	3	817-1689/3	GTR + G	3	580-1230/3	GTR + G
mtMutS – 2nd	3	818-1689/3	GTR + G	1	581-1230/3	HKY + I + G
mtMutS – 3rd	4	819-1689/3	SYM + G	3	582-1230/3	GTR + G
16S	1	1690-2033	GTR + I + G	1	1231-1515	HKY + I + G
18S	1	2034-3808	GTR + I + G	4	1516-3115	K80 + I + G
28S	5	3809-4674	GTR + I + G	5	3116-3561	K80 + I + G

are described in Appendix A. PCR success was verified using gel electrophoresis before strong amplifications were sent to Macro-gen Europe (Amsterdam, Netherlands) for sequencing in both directions. All chromatograms were visualised and sequence pairs matched and edited in Geneious 6.1.7 (Biomatters, Ltd., Auckland, New Zealand). GenBank sequence accession numbers are listed in Appendix B.

### 2.3. Gene alignment

Given that incomplete (too few) character data, rather than missing data, seems to be an important factor in accurate phylogenetic reconstruction (Wiens, 2003), and utilising even highly incomplete taxa can still be beneficial (Wiens and Tiu, 2012), we retained all specimens with sequences from 2 genes or more in the analyses. This resulted in 176 specimens in final phylogenetic analyses.

Initial alignments were undertaken using ClustalW with default settings in Geneious 6.1.7 (Biomatters Ltd.). Alignments were checked and edited by eye. Accurate alignments are crucial in ensuring accurate phylogenies and for this reason the variable *igr* region of *cox1* (133–150 nt in length) was removed from analyses.

Alignments were also submitted to the Gblocks server (Castresana, 2000). For protein-coding genes, default settings were used. For 16S, 18S, 28S the less stringent “allow less strict flanking positions” was selected. Alignment details are listed in Table 2.

### 2.4. Phylogenetic analyses

The alignment was submitted to PartitionFinder (Lanfear et al., 2012) to evaluate the best partition schemes and associated substitution models under BIC criteria. Out of 96 schemes a 5-partition model was selected. That partition was tested against user-defined alternative models (for example linking the first two codons of protein-coding genes in one partition); the 5-partition scheme retained the highest scores under BIC.

Phylogenies were determined using two methods: maximum likelihood (ML) and Bayesian Inference (BI). ML analyses were performed using RAxML v.7.2+ (Stamatakis, 2014) and BI analyses were performed using MrBayes v.3.2 (Ronquist et al., 2012), both on the CIPRES Science Gateway (Miller et al., 2010). Under BI analyses, using the models of evolution listed in Table 2, Metropolis-coupled Monte Carlo Markov Chains (MCMC) were run for 30 million generations ( $\times 8$  chains, temp = 0.05) with trees sampled every 1000 generations. The parameters of nucleotide frequencies, substitution rates, gamma shape, and invariant-sites proportion were unlinked across partitions. To account for the rate variation among partitions (Marshall et al., 2006), we allowed rates to vary under a flat Dirichlet prior distribution (ratepr = variable). Convergence was obtained if the standard deviation of partition frequencies was <0.01, the potential scale reduction factor PSRF

was  $\sim 1.00$ , the effective sample sizes (ESS) were >200, and if the shape of the stationary posterior-distribution trace (generations vs. LnL) of each parameter was a “straight hairy caterpillar” (Drummond et al., 2007) when visualised in TRACER v1.6 (Rambaut and Drummond, 2007). Resulting trees were summarized into a 50% majority tree in MrBayes. ML analyses were generated under 5-partitions, random trees were used and all other default parameters were kept. For the latter, analyses were performed under the GTR + I + G model of evolution as this is available in RAxML. One thousand pseudoreplicate bootstraps were performed to test tree robustness. Each analysis was performed at least twice to verify the repeatability and reliability of outputs. Each gene, combined nuclear, and combined mitochondrial datasets were run separately, and both with and without GBlocks. Trees were rooted using *Cornularia pabloi* as this genus has been shown to be in a sister group to all other Octocorallia (analysis using *cox1*, *mtMutS*, 28S; McFadden and van Ofwegen, 2012).

### 2.5. Time estimation of sub-Antarctic divergence using fossil calibration

BI analysis of divergence time was undertaken with BEAST v.1.7.5 (Drummond and Rambaut, 2007) using a subset of 89 specimens from phylogenetic analyses to speed up processing time. Preliminary analyses showed the partitioned dataset was over-parameterised. Whole genes (rather than codon position partitions) were submitted to JModeltest. The optimal model of sequence evolution for *cox1*, 16S, 18S and 28S was found to be the general time reversible model of evolution with  $\Gamma$  distributed-rate heterogeneity and an estimated proportion of invariable sites (GTR + I +  $\Gamma$ ) as determined by Bayesian Information Criterion in Modeltest; *mtMutS* was found to have a GTR +  $\Gamma$  model of evolution. An uncorrelated log-normal relaxed clock model was set. Substitution models and clock models were unlinked across partitions. Each MCMC chain was started with a tree topology from the reduced dataset under the same BI specifications as the above phylogenetic analyses. Four independent runs of 100 million generations were performed, twice; one of which is displayed here. Runs were considered complete with ESSs of >150 for all parameters. Trees were sampled every 5000 generations and 10% of each run removed as burn-in using Logcombiner v.1.8.0 (Rambaut and Drummond, 2013). TreeAnnotator was utilised to summarise resulting tree samples into a single consensus tree using the “maximum clade credibility” and mean height options.

### 2.6. Fossil calibration justification

The multi-element nature of many octocoral skeletons means they degrade quickly post-mortem making their presence in the fossil record relatively rare (reviewed in Schlagintweit and Gawlick, 2009; see also Whittle et al., 2014). Dates listed below

are according to the most recent advice from the International Commission on Stratigraphy (Gradstein et al., 2012).

*Echmatocrinus brachiatus* has a disputed taxonomy, originally being described as a member of Crinoidea (Sprinkle, 1973; Sprinkle and Collins, 1995, 1998), and later tentatively placed within Octocorallia, with a suggestion that it is a Primnoidae (Ausich and Babcock, 1998; reasserted in Ausich and Babcock, 2000). Being from the third series of the Cambrian, 509–500 MYA (million years ago), this would be the earliest known octocoral, however, its taxonomy is widely debated and thus not used in analyses.

The earliest undisputed fossil octocoral is an Alcyonacea (Order) speculated to be of the Suborder Holaxonia (Cope, 2005) from the Early Ordovician, 470–485 MYA. There are many calcified holdfasts in the fossil record (Giammona and Robert, 1980; Malecki, 1982; Stolarski, 1996). However, holdfasts occur across a range Holaxonia families (Gorgoniidae, Plexauridae, Acanthogorgiidae, Keroeididae) and in Calcaxonina (Primnoidae, Isididae, Chrysogorgiidae, etc.), which are both polyphyletic (McFadden et al., 2006; McFadden and van Ofwegen, 2012), so it is not possible to use these fossils.

There are some very early fossil sclerites from the upper Llandoveryan to Lower Wenlockian, 435–430 MYA, that may represent a species of Alcyoniidae (Bengston, 1981). However, phylogenetic analyses have suggested Alcyoniidae are polyphyletic (McFadden et al., 2006; McFadden and van Ofwegen, 2012; Park et al., 2012; McFadden and van Ofwegen, 2013), so again it is also not possible to use this date accurately in calibrations.

The earliest known *Corallium* fossil is *C. elegantum* Kuzmicheva, 1987, from the Campanian-Maastricht series in the Cretaceous (Schlagintweit and Gawlick, 2009). This stage age ranges from 83.6 to 66 MYA. Pennatulacea (seapens) have been recorded from the Campanian-Maastrichtian, 83.6–66.0 MYA, and they are well known from the Late Cretaceous period (reviewed in Reich and Kutscher, 2011). There is one putative, and unusual, recently reinterpreted specimen called *Pywackia baileyi*, from the upper Cambrian/Furongian, 497–485 MYA, that, although not a true seapen, could be a precursor to this lineage (Taylor et al., 2013b); if so, it would be the earliest known fossil Octocorallia. The origin of Pennatulacea are keenly debated, with Williams (1997) suggesting that seapens developed from a soft coral, similar to the present-day alcyoniid *Anthomastus*; and genetic evidence suggests *Anthomastus* is closely related to seapens, though not a sister grouping (McFadden et al., 2006). The earliest appearance of an Isididae in the fossil record is *Isis ramosa* from the Campanian, 72.1–83.6 MYA (Helm and Schülke, 2003).

Considering the disputed nature of several of the fossils discussed above we undertook two analyses:

1. Conservative: With *Corallium* and Pennatulacea node dates of 83.6–66.0 MYA and Isididae at 72.1–83.6 MYA.
2. Speculative: With an older node date for Pennatulacea of 497–485.4 MYA, based on *Pywackia baileyi* (Taylor et al., 2013b), *Corallium* at 83.6–66.0 MYA and Isididae at 72.1–83.6 MYA with the above ingroup and prior distributions applied.

A lognormal prior distribution for the above dates was used where the offset was the youngest age and the 97.5% quartile of the upper age of the stratum under consideration.

### 3. Results

#### 3.1. Data summary

Of the 176 specimen sequences, 43 (24%) were taken from GenBank meaning their alignments usually included just 2 or 3

**Table 3**

Sequence coverage per gene for the 176 specimens.

Gene >	<i>cox1</i>	<i>mtMutS</i>	16S	18S	28S
No. of specimens with no sequence data	9	6	61	17	52
% of specimens with no sequence data	5	3	34	10	30

genes. Sequence coverage per gene is listed in Table 3. Alignments had, on average, 20% missing data (median 18%) – with a maximum of 66% (specimen missing data breakdown in Appendix B, Table B1). The total dataset of *cox1* (without igr), *mtMutS*, 16S, 18S and 28S contained 4674 nucleotides (GBlock dataset = 3561).

#### 3.2. Phylogenetic analysis results

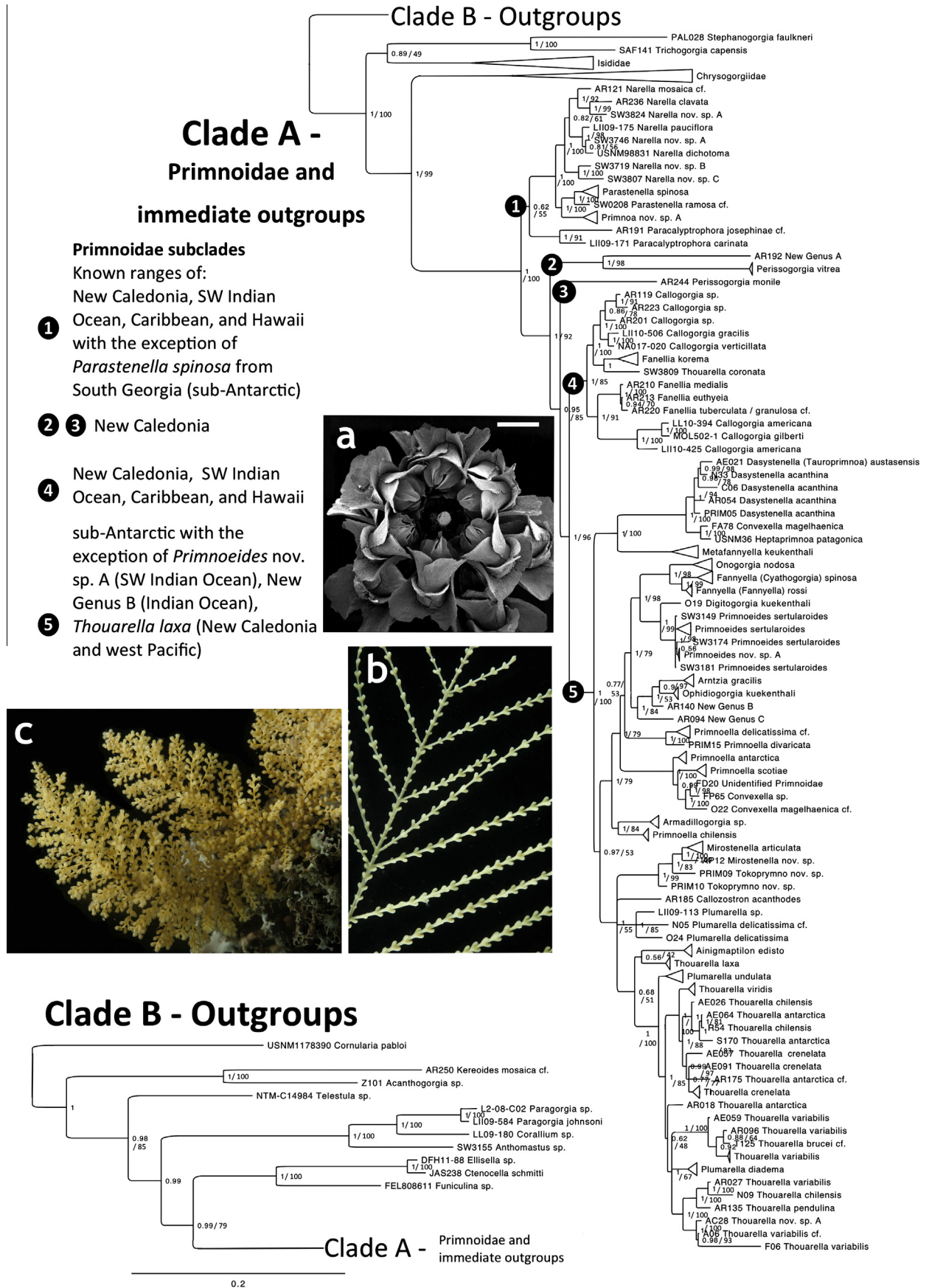
All individual gene phylogenetic trees showed some of the major species level clades but little resolution or structure in deeper relationships, at family level (results not presented here). Near identical tree topologies were found using all-genes with both ML and BI analyses and with and without GBLOCKS (results without GBlock are presented here). As is common, BI analyses had stronger node support than ML. BI trees are presented here with node-support values from both ML and BI. Nuclear gene only trees were a large polytomy. The major clade groupings in the mitochondrial gene only trees were identical to Figure 1 with the exception that *Thouarella coronata* (SW3809) was not embedded within a clade with *Fanellia* and *Callogorgia* but sister to said clade.

The wider sampling of Primnoidae in this analysis means we can say with some confidence that this family is monophyletic, as previous studies have found (McFadden et al., 2006; Pante et al., 2012). Chrysogorgiidae are sister to Primnoidae in a well-supported clade.

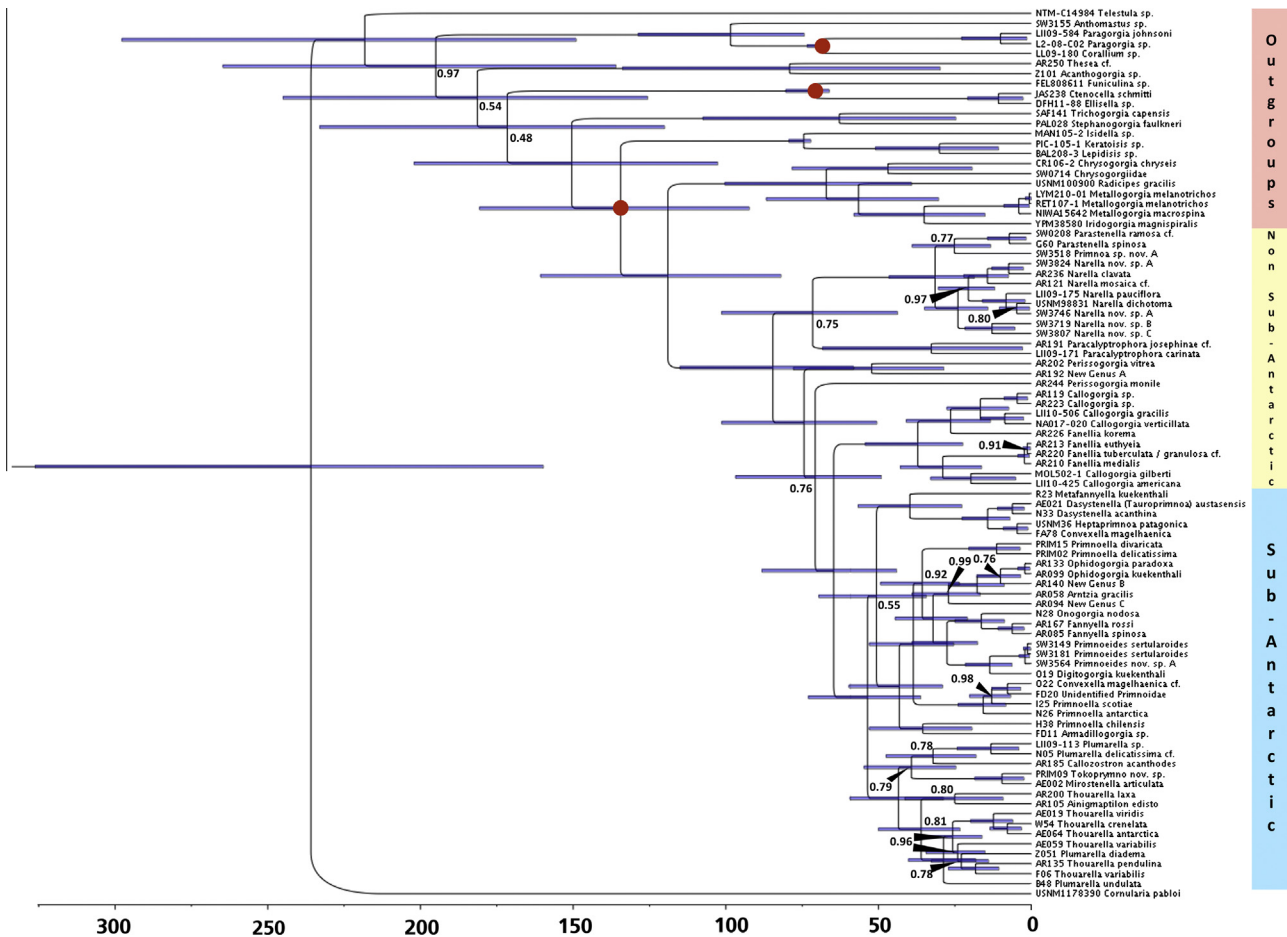
Within Primnoidae there are 4 well-supported clades (Fig. 1) with A1 being weakly separated from remaining clades. A1 is a mix of genera with samples originating from New Caledonia (*Paracalyptrophora josephinae* is tentatively identified and could expand this know range from the Atlantic to New Caledonia), the southwest Indian Ocean, Hawai'i and the Gulf of Mexico, with two specimens of *Parastenella spinosa* from South Georgia (the only sub-Antarctic specimen in this clade). The second clade (A2) is made up of specimens from New Caledonia: a specimen of New Genus A and two specimens of *Perissogorgia vitrea* (falling separate to a specimen of *P. monile*, A3). The third clade (A3) is a solitary sample of *Perissogorgia monile* from New Caledonia. The specimens in A4 are from a range of locations (Hawai'i, New Caledonia, Portugal, Gulf of Mexico) but none are from the sub-Antarctic. The fifth clade (A5) is a large collection of specimens originating from the sub-Antarctic with the exception of three sets of specimens: 1. New Genus B (AR140), which is the deepest specimen in the analysis, from 4500 m depth in the Indian Ocean, 2. specimens of *Primnoeides* from the southwest Indian Ocean, and, 3. *Thouarella laxa* from New Caledonia.

In this analysis, most genera are represented by just one species. For those with two species represented, many genera are monophyletic and well-supported (*Narella*, *Parastenella*, *Paracalyptrophora*, *Dasystenella*, *Primnoeides*, *Mirostenella*, *Fannyella* – see Systematic Results for discussion of *Metafannyella*). That said, several other genera with two or more species represented are polyphyletic (*Callogorgia*, *Fanellia*, *Primnoella*, *Plumarella*, *Thouarella*), indicating that with more taxon sampling the monophyly of the former listed genera may not be retained.

As mentioned above, several genera are polyphyletic. The two species of *Perissogorgia* cluster towards the base of the major clade of mostly sub-Antarctic Primnoidae (A5), but in separate clades. Species of *Fanellia* were once taxonomically placed within



**Fig. 1.** Maximum Likelihood (ML) and Bayesian Inference (BI) phylogenetic analyses of a five-gene concatenated dataset with 5 partitions. Node support values represent BI/ML posterior probabilities. (a) Whorl of polyps, anterior view, *Narella* sp. nov.; (b) section of colony of *Primnoeides sertularoides*; and (c) colonies of *Thouarella* sp.



**Fig. 2.** Bayesian analysis of ‘conservative’ concatenated gene data (no GBlocks) performed using BEAST. If no node label then posterior probability support was 1. Node bars show 95% highest posterior densities (HPD) for the time divergence estimates. Red circles indicate fossil calibration nodes. Numbers across the base are millions of years. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

*Callogorgia*, but were separated by Bayer (1982) on the basis that the sclerites of *Fanella* are “sculptured externally by closely set, angular tubercles” (Bayer, 1982, p. 135), which is not seen in *Callogorgia* (which has species with body-wall scales that are smooth or sculptured externally by radial crests distally); the analysis presented here has them in a mixed clade bringing into question, in this instance, the reliability of external sclerite sculpture in genera designation. Two of the genera with true ascus scales (*Fannyella*, *Onogorgia*) are, however, found in a clade together.

*Primnoella* is polyphyletic, being found in clades with *Armadillogorgia* and *Convexella*. The genus *Primnoella* requires revision.

The *Thouarella laxa*–*Ainigmaptilon* separation from remaining *Thouarella* and *Plumarella* is weakly supported. We were not able to amplify either 18S or 28S for any samples of *Ainigmaptilon*. However, these analyses do confirm that *Ainigmaptilon*, after debate (summarised in Cairns and Bayer 2009), belongs within the Primnoidea (Bayer, 1981).

In these analyses, both specimens of *Thouarella* from outside the sub-Antarctic (*T. coronata* from the southwest Indian Ocean and *T. laxa* from New Caledonia and the west Pacific) are found in separate locations on the phylogenetic tree. The latter, *T. laxa*, is embedded within the sub-Antarctic clade of Primnoidea.

Bayer did not distinguish *Ainigmaptilon* and *Callozostrom* in his 1981 octocoral key as he believed both had partially fused polyp bases, like “polyp leaves” (the specific differences and similarities are discussed in Bayer, 1996, p. 151); our analyses find these genera do not cluster together, however, we would like to have nuclear

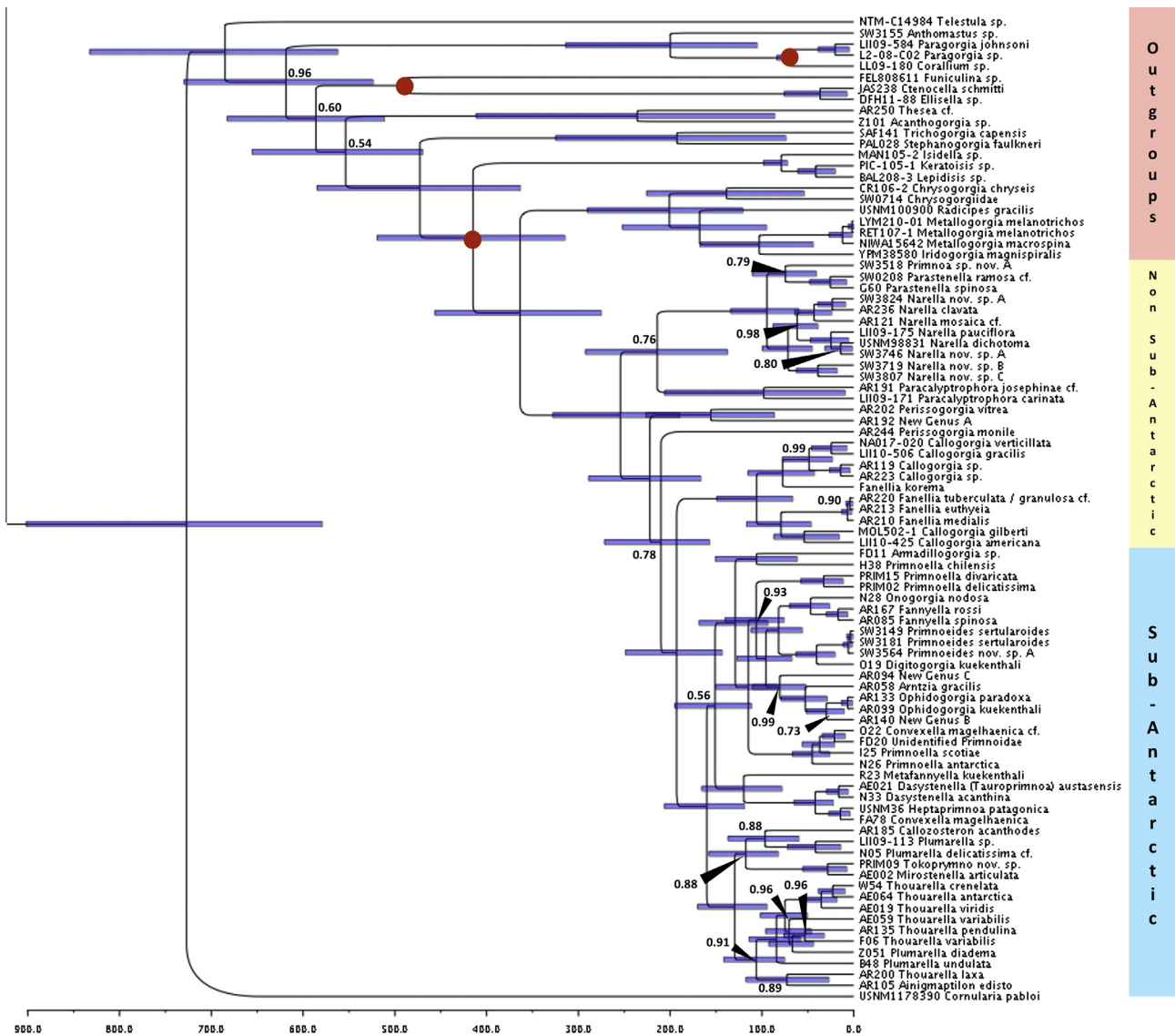
genes for the former and 18S for the latter to confirm the relative placement of these genera.

Several authors have discussed primnoid character evolution (Kinoshita, 1908a; Versluys, 1906; Cairns and Bayer, 2009). Both Versluys (1906) and Kinoshita (1908) thought it evolutionary advantageous for polyps to have fewer and larger scales on polyps. Our analyses do not support this character evolution as genera with relatively few, large scales, such as *Dasystemella* and *Narella*, are found in different areas of the tree. And the smooth, small and irregular placement of scales in *Primnoeides* was also suggested as an ancestral form (Versluys, 1906; Kükenthal, 1919), and phylogenetic analysis of Primnoidea morphological characters placed this genus basal to all other primnoid genera (Cairns and Bayer, 2009); data presented here suggests these characters are derived.

This analysis confirms that organic gorgonin nodes/internodes, a key taxonomic character, have developed at least three times within Octocorallia: in Isididae (bamboo corals), *Mirostenella*, a genus of Primnoidea, and Melithaeidae. Although no Melithaeidae were within this analysis previous studies have placed them separate to Primnoidea and Isididae (McFadden and van Ofwegen, 2012).

### 3.3. Fossil calibration analysis results

With the limited number of fossil calibration points in these analyses resulting dates should be treated with caution. For each



**Fig. 3.** Bayesian analysis of ‘speculative’ concatenated gene data (not GBLOCK) performed using BEAST. If no node label then posterior probability support was 1. Node bars show 95% highest posterior densities (HPD) for the time divergence estimates. Red circles indicate fossil calibration nodes. Numbers across the base are millions of years. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

analysis, all four independent runs converged on similar distributions of MCMC run giving some confidence of the resulting crown dates. Our conservative analysis (Fig. 2) found 95% highest posterior densities (HPD) for the time divergence estimates of Primnoidae from other octocorals to be between 81 and 160 MYA (mean of 116 MYA), the mid-Cretaceous to late Jurassic. Speculative analysis (Fig. 3) found this date pushed back to between 275 and 456 MYA (mean of 359 MYA).

When considering radiation of the sub-Antarctic Primnoidea clade (A5) the Conservative and Speculative analyses also had vastly different timings. The Conservative analysis had an estimated sub-Antarctic Primnoidea radiation of 52 MYA (95% HPD: 36–73 MYA). With an older speculative crown age the radiation date was pushed back to a mean date of 157 MYA (95% HPD: 118–204 MYA).

#### 3.4. Primnoidea systematic results

*Plumarella* was not recovered as monophyletic; specimens of this genus were in a mixed clade with species of *Thouarella*.

*Plumarella diadema* and *P. undulata* were recently moved to *Plumarella* from *Thouarella* (Cairns, 2011), based on the lack of keel on their marginal scales. This character is the only morphological feature that currently splits these two genera, however, the character is one that can have a range of acuteness, from smooth to furrowed (as in *P. diadema* and *P. undulata*) to truly keeled (as found in *Thouarella*). A wider sampling of *Plumarella* and *Thouarella* species is required to delineate characters that separate these genera and it has long been suggested that a *Plumarella* revision is necessary.

*Thouarella* species were recently split into two species groups – Group 1 species have isolated polyps and Group 2 has polyps in whorls (Taylor et al., 2013a). The historical taxonomic groupings of ‘Antarctica’ and ‘Köllikeri’ species are not separate in the presented phylogenies making the recent merging of these groups (discussed in Taylor et al., 2013a) into Group 1 (species with isolated polyps) supported by this phylogenetic analysis. Only one species from Group 2 (*Thouarella coronata*) is in this analysis and does not cluster with Group 1 *Thouarella*; more species are required to comment further on the validity of the *Thouarella* species groups and if they should be raised to subgenera level.

More informative genetic markers may be required as some *Thouarella* species (Fig. 1) are mixed, inferring that morphological variability is present that is not seen in the genetic data. Conversely, there are also polyphyletic *Thouarella* species; this infers there may also be genetic variability the morphological characters for which are currently not identified.

Suggested adaptations to current Primnoidea systematics are suggested here.

#### 3.4.1. *Metafannyella kuekenthali* (Molander, 1929) new combination

*Fannyella kuekenthali* Bayer, 1998, pp. 188–195, Figs. 37–52; Cairns and Bayer, 2009, p. 28 [listed]

*Caligorgia kükenthali* Molander, 1929, p. 62, Figs. 15, 16, pl. 1, Fig. 3

?*Caligorgia ventilabrum*, Molander, 1929, p. 62.

3.4.1.1. *Material examined.* BAS-06-0930-08 (Oxford sub-sample AC08), BAS-06-0930-17 (Oxford sub-sample AC19), BAS-06-0930-19 (Oxford sub-sample AC19), JR 144 BIOPEARL, sta. SR-AGT3, South Georgia, –53.58541°, –40.92084°, 450–467 m, 11th April 2006; S11, Argos *Froyanas*/MRAG, set 20, sample 9, South Georgia, –53.23°, –42.70°, 1197–1227 m, 2007; Z25, *Jacqueline*/MRAG, set 25, sample 23, South Georgia, –53.875°, –39.7°, 1110–1245 m; G03, Argos *Helena*/MRAG, set 36, sample 5, South Georgia, –53.78°, –42.23°, 1215–1463 m.

3.4.1.2. *Description.* Recent genus description in Cairns and Bayer (2009), species description in Molander (Molander, 1929) and in-depth species level discussions in Bayer (1998).

3.4.1.3. *Distribution.* Circum-Antarctic.

3.4.1.4. *Discussion.* In 2009, Cairns and Bayer separated members of *Fannyella* with weakly ascus scales into a new genus, *Metafannyella*. Bayer (1998) extensively illustrated *Fannyella kuekenthali* and we suggest this species too has weakly ascus scales and should therefore be referred to as *Metafannyella kuekenthali*. This new combination is supported by our phylogenetic analysis and makes *Fannyella* monophyletic, however, wider genetic taxon sampling is required to confirm the latter.

#### 3.4.2. *Dasystenella Versluys, 1906*

*Stenella* Wright and Studer, 1889:59 [*S. acanthina*]

*Stenella* (*Dasystenella*) Versluys, 1906, p. 39, 48.

*Thouarella*, Kükenthal, 1915, p. 151, 1919, p. 441, 1924, p. 302.

*Dasystenella* Bayer, 1981, p. 934, 937, 946 [key to genus]; Bayer and Stefani, 1989, p. 454 [key to genus], Cairns, 2006, pp. 188–189; Cairns and Bayer, 2009, p. 32 [listed], 47–49, fig. 18 i–p; Taylor et al., 2013, pp. 99–102, Figs. 39a–n.

*Tauroprimnoa* Zapata-Guardiola and López-González, 2010, pp. 314–317, Figs. 2–6.

*Dasystenella austasensis* Zapata-Guardiola and López-González, 2010, new combination

*Tauroprimnoa austasensis* Zapata-Guardiola and López-González, 2010, pp. 314–317, Figs. 2–6

3.4.2.1. *Dasystenella austasensis.* (Zapata-Guardiola and López-González, 2010), new combination.

3.4.2.2. *Material examined. Paratype, Tauroprimnoa austasensis* (USNM 1128573) ANTXXI/2, stn. PS65/292-01, 72°51.43'S 19°38.62'W, Austasen, Eastern Weddell Sea, Antarctica, 596.4–597.6 m depth, 31 December 2003. AE021, R/V *Sil*, set 8, South Georgia, –53.79°S, –40.88°S, 234–257 m, 28th May 2005, 2 colonies;

E19, R/V *Isla Santa Clara*, set 40, sample 35, South Georgia, –55.25°S, –36.325°S, 1310–1720 m.

3.4.2.3. *Description.* Recently described by Zapata-Guardiola and López-González (2010b).

3.4.2.4. *Comparisons.* Our phylogenetic analysis places *Tauroprimnoa* Zapata-Guardiola and López-González, 2010, within a clade alongside *Dasystenella* Versluys, 1906. A number of specimens of *Dasystenella* showed very low genetic variability when compared to 2 specimens of *Tauroprimnoa* (one in this analysis). Reassessment of the original description and examination of paratype material supports *Tauroprimnoa austasensis* as a species of *Dasystenella* with the subtle change that the primary abaxial body-wall scale on polyps of this species are considered to be a reduced marginal scale with a rounded distal edge (rather than the elongated marginal seen in the only other species of *Dasystenella*, *D. acanthina*). With 5 marginal scales this species is therefore recommended as more appropriately placed within *Dasystenella*. The authors studied specimens with polyps bearing 5 long marginal scales, *D. acanthina*, and, on the same colony, those with 4, as seen in *D. austasensis*; this suggests that the two current species of *Dasystenella* may be one species with wide morphological variation. However, until higher resolution genetic analysis is undertaken, and to ease identification of these morphological variants, we suggest that colonies with more than 50% of their polyps bearing 4 marginals should be considered *D. austasensis* and the remainder of specimens as *D. acanthina*.

## 4. Discussion

### 4.1. Evolutionary history of Primnoidea

Distance, deep water, sub-zero temperatures, and the strongest current system in the world (the Antarctic Circumpolar Current – ACC) isolate Antarctic waters. The ACC flows clockwise, extending from the surface to 4000 m depth, and can be 2000 km wide (Lebedev, 2006). There is some debate about the timing of the ACC onset (Pfuhl and McCave, 2005; Barker et al., 2007) with recent suggestions that shallow flow across the Drake Passage commenced in the early Eocene (41–37 MYA; Scher and Martin, 2004), and slowly developed, deeper, through the Oligocene (up to 23 MYA; Livermore et al., 2007; Katz et al., 2011). Our 'Conservative' analysis suggests that the expansion of sub-Antarctic Primnoidea (mean of 52 MYA) pre-dates the initiation of the ACC; meaning this fauna have been *in situ* for an extensive period of time and over a large range of environmental conditions. Before this time, in the late Cretaceous (the “greenhouse world”), the oceans were warmer (Haupt and Seidov, 2001; Otto-Bliesner et al., 2002), cooling through the early Cenozoic (Paleogene), into our modern “icehouse” climate (Norris et al., 2013; Zachos et al., 1994). At the beginning of the period when sub-Antarctic Primnoidea are believed to have radiated in our 'Conservative' analysis (with the recognised limitations of just 3 calibration points; Sauquet et al., 2012) deep ocean temperatures would have been 8–12 °C (Haupt and Seidov, 2001), much warmer than the 1–3 °C found in the modern Antarctic ocean (Norris et al., 2013). There is evidence for a pre-ACC origin of a number of Antarctic marine invertebrates (Clarke and Crame, 2010): isopods and Ostracoda (Brandt, 1999), amphipods (Watling and Thurston, 1989), and molluscs (Beu, 2009). The relevance of refugia in times of glacial maxima to current population structures is keenly debated (Allcock and Strugnell, 2012; Convey et al., 2009; Thatje et al., 2005, 2008). Genetic evidence presented here suggests that Primnoidea survived through these glacial disturbances and, as



discussed in Crame (2013), given the warm and relatively even climate before the ACC onset, temperature would not appear to drive this early radiation. A latitudinal gradient in seasonality has been suggested as a more important factor in early polar fauna evolution, something that may have been enhanced by late Cenozoic temperature decline (Crame, 2013).

Under ‘Speculative’ fossil-calibration estimates, sub-Antarctic Primnoidae radiated in the late Jurassic (mean of 157 MYA). The late Jurassic is also believed to have had ‘greenhouse’ conditions, with temperatures warmer than at present (Sellwood et al., 2000). There is much debate on the origin of the Pennatulacea and with the unusual, albeit convincing, similarity to the present-day seapen *Lituaria*, conclusions that *Pywackia baileyi* is a true seapen are not certain (Taylor et al., 2013b). Conversely, a recent fossil-calibrated analysis of Cnidaria (Park et al., 2012) dated the divergence of Octocorallia from Hexacorallia in the late Cryogenian (819–544 MYA), so perhaps such an aged octocoral tree is possible. However, *Pywackia baileyi* may well be on a different lineage to present-day seapens. Unfortunately the limited fossils available and resulting large time estimations make confidence in either scenario low.

With 60 of 266 species (23%) being found in the sub-Antarctic, Primnoidae can be added to the growing list of benthic organisms that have rich Southern Ocean biodiversity. The Southern Ocean is widely recognised as an evolutionary centre of origin for many marine species (Crame, 1993; Briggs, 2003; Strugnell et al., 2008). However, the non-Antarctic base to the Primnoidae would suggest that the large number of species within the sub-Antarctic is a secondary *in situ* radiation (Fig. 1, A5); meaning that the sub-Antarctic is not the origin for this speciose family, as has been previously suggested (Cairns and Bayer, 2009; Taylor et al., 2013a). For Primnoidae at least, Antarctica is mostly an evolutionary sink, rather than a source (Crame, 1993; Briggs, 2003), with diffusion from the deep oceans of the tropics to the Antarctic, so-called “polar emergence” – as seen in *Benthoctopus* (Strugnell et al., 2011), the deep-sea holothurian, *Elpidia* (Mironov et al., 2013), Pleurobranchinae (Göbbeler and Klusmann-Kolb, 2010) and crinoids (Eléaume et al., 2012). Our analyses suggest, acknowledging that not all species are included, that Primnoidae originated in the Pacific.

There is wider evidence of both Antarctic emergence (listed above) and submergence (e.g. octopus – Strugnell et al., 2008; isopods – Brandt et al., 2007; Raupach et al., 2009; crinoids, Eléaume et al., 2012). Here we present genetic evidence for submergence at lower latitudes occurring at least four times in Primnoidae; *Primnoeides* specimens and ‘New Genus B’ (AR140 – the deepest specimen in the analysis at 4500 m) were found in the Indian Ocean, and are embedded within the sub-Antarctic Primnoidae clade. Similarly, *Thouarella laxa* from New Caledonia and the west Pacific, was also embedded within this clade, suggesting this species is a recent submergence event into this region from the sub-Antarctic. *Parastenella spinosa* is the only sub-Antarctic specimen within a clade of specimens from a range of different locations (Fig. 1, A1) such as New Caledonia and SW Indian Ocean; this could be evidence of another submergence event.

## 5. Conclusions

Given that climate change is likely to effect the poles to a greater extent than other marine regions (Meredith and King, 2005; Orr et al., 2005; Whitehouse et al., 2008) it is important to understand the evolutionary history of organisms that exist, and thrive, there. This research presents evidence that, although likely having a non-Antarctic origin, Primnoidae have radiated successfully through this region, and then submerged into the deep waters of other oceans. The timings of the sub-Antarctic radiation of Primnoidae are still debatable; our data suggests this occurred before the onset of the ACC. Discovery of additional fossils with lower taxonomic identifications will be needed to help clarify the evolutionary history of this key and “quintessential” member of deep-sea benthic communities.

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**Table A1**  
PCR conditions and primers used.

Primer name (gene)	Primer sequence 5' > 3'	Fragment size (bp)	(Initial Temp:Time) (Annealing Temp:Time) (Extension Temp:Time)	No. of cycles/(Final Extension Temp:Time)	Reference
COI18068F (cox1)	CCATAACAGGACTAGCAGCATC	1100	(94:30) (59:90)	35/(72:300)	McFadden et al. (2004)
COIOCTR (cox1) ND42599F (mtMutS)	ATCATAGCATAGACCATAACC GCCATTATGGTTAACTAATTAC	870	(72:60) (94:60) (45–58:45–90)	35/(60:1800)	F: France and Hoover (2002)
Mut3458R (mtMutS) Octo1-L (16S)	TSGAGCAAAAGCCACTCC AGACCCTATCGAGCTTACTG	630	(65–72:60) (94:30) (51:60)	30/(72:600)	R: Sanchez et al. (2003) France et al. (1996)
Octo2-H (16S) 18S-Af (section 1)	CGATTAGAACTCTCCGACAATA AACCTGGTTGATCCTGCCAGT	620	(72:180) (94:20) (58:30) (72:40)	40/(72:600)	F: Modified by Pante et al. (2012), originally from Medlin et al. (1988)
18S-Lr (section 1) 18S-Cf (section 2)	CCAACTACGAGCTTTTAACTG CGTAATTCCAGCTCCAATAG	710	(94:20) (57:30)	35/(72:600)	R: Apakupakul et al., 1999 Apakupakul et al. (1999)
18S-Yr (section 2) 18S-Of (section 3)	CAGACAAATCGCTCCACCAAC AAGGGCACCACCAGGAGTGGAG	620	(72:40) (94:20) (58:30)	35/(72:600)	F: Apakupakul et al. (1999)
18S-Br (section 3)	TGATCCTCCGAGGTTACCT		(72:40)		R: Modified by Pante et al., 2012, originally from Medlin et al. (1988)
Far (28S)	CACGAGACCGATAGCGAACAAGTA	810	(94:30) (54:90)	35/(72:600)	Adapted from McFadden and van Ofwegen (2012)
Rar (28S)	TCATTTCGACCCTAAGACCTC		(72:60)		

Temperatures in °C. Time in seconds. F = forward primer, R = reverse primer.

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## Appendix A

See Table A1.

## Appendix B. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ympev.2014.11.008>.

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